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Inheritance of morpho-agronomic traits in ornamental peppers (*Capsicum annuum* L.)

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Abstract

Peppers have shown an increasing and continuous acceptance by the consumer market, standing out in the trade of potted ornamental plants. From this perspective, this study aimed to estimate the genetic parameters and genetic effects involved in the inheritance of traits referring to plant size, flowers, and fruits in a segregating generation of ornamental pepper plants (*Capsicum annuum* L.). The experiment was conducted in a plant nursery. Two ornamental pepper (*C. annuum* L.) accessions belonging to the vegetable germplasm bank of the Federal University of Paraíba (UFPB) were used as parents: UFPB 349 and UFPB 356. The experimental design was completely randomized, with five plants of each parent, 20 plants of generation F1, 88 plants of generation F2, and 40 plants of the backcross generations BC1 and BC2. Nineteen quantitative traits referring to plant, flowers, and fruits were evaluated. The data obtained were subjected to generation analysis, and the effects of the models were subjected to the t-test at 5% and 1% of significance. Highers broad- and narrow-sense heritability values were observed for plant height and pericarp thickness, suggesting the predominance of additive genetic effects in trait expression. The additive-dominant model (m, a, d) was suitable (r-value superior to 0.7) to explain the genetic parameters of most traits. However, for canopy diameter, petal diameter, pedicel length, and dry matter content, the additive-dominant model was inadequate, and the interpretation of the complete model is recommended instead.

Keywords: *Capsicum annuum*, gene interaction, heritability

Introduction

The pepper-consuming market has grown considerably in recent years due to the multiple applications and forms of use of this product (Rêgo et al., 2012a; Santos et al., 2013), with the annual pepper trade corresponding to approximately 17% of the total worldwide spice trade (Navhale et al., 2017).

In Brazil, the pepper market has acquired considerable significance in the economic scenario, especially due to the great variety of products such as sauces, jellies, and exotic jams, in addition to ornamental use (Rêgo et al., 2012a; Sudré et al., 2010; Valnir Júnior et al., 2015).

The genus *Capsicum* shows high genetic diversity for traits such as shape, size, color, and position of flowers and fruits (Bianchi et al., 2016). This variability can be used to obtain new varieties in response to the growing market demand (Rêgo et al., 2009a; 2011a; 2012b). Furthermore, fruit color and plant architecture are the main traits used in the breeding of ornamental peppers (Rêgo et al., 2009b; 2012b), and developing improved cultivars for the several species of this genus is promising to widen and sustain the pepper agribusiness (Moura et al., 2010).

The potential of the base population and the efficiency of selection can be investigated by quantifying the importance of additive, dominance, and epistatic effects for each trait (Bento et al., 2016). In this scenario, generation analysis allows evaluating the suitability of the additive-dominant model to a given trait and estimating genetic parameters based on means and variances (Cruz, 2012).

From this perspective, this study aimed to estimate the genetic parameters and genetic effects involved in the inheritance of morpho-agronomic traits in ornamental pepper plants (*Capsicum annuum*).

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Material and Methods

The experiment was conducted in a plant nursery at the Laboratory of Plant Biotechnology of the Center of Agricultural Sciences (CCA) of the Federal University of Paraíba (UFPB), Areia - PB.

The plants used as parents were two ornamental pepper accessions (*Capsicum annuum* L.) from the vegetable germplasm bank of the Federal University of Paraíba (BGH-UFPB): UFPB 349 and UFPB 356. These accessions were selected based on a previous study, and their characteristics are shown in Table 1. Parents 349 and 356 were crossed to obtain the F_1 generation, from which the F_2 generation was obtained by self-fertilization. The backcross generations BC_1 and BC_2 were obtained by crossing F_1 with the P_1 and P_2 parents, respectively.

Table 1. Parent traits used to obtain the F_1, F_2, RC_1, and RC_2 generations.

Traits	Parents	
	UFPB 349	**UFPB 356**
Stem color	Green	Purple
Leaf color	Green	Variegated
Flower color	White	Purple with a white base
Anthocyanin on the fruit	Absent	Present
Fruit color at intermediate stages	Light green/Orange	Green/Dark Purple/Orange
Mature fruit color	Red	Red

The crosses were performed in the plant nursery. First, the flower buds were emasculated before anthesis, after which the flowers were pollinated by pollen conduction from one plant to the stigma of the receiving flower. Then, the flowers were identified with tags and covered with aluminum foil (Nascimento et al., 2012; Rêgo et al., 2012a; 2012c). The mature fruits were harvested one to two months after pollination, after which the seeds were removed.

The parents (P_1 and P_2), their progeny (F_1), the segregating generation (F_2), and the backcrosses (BC_1 and BC_2) were sown in polystyrene trays with 128 cells filled with the commercial substrate Plantmax® containing two seeds per cell. The tray was kept in a shaded environment until seedling emergence. When the seedlings had from four to six true leaves, about 50 days after sowing, they were transplanted to 900-mL plastic pots and grown in the plant nursery.

The morpho-agronomic characterization was performed based on the list of descriptors suggested by *Biodiversity International (IPGRI, 1995)* by evaluating ten quantitative traits referring to plant, flower, and fruit. Plant height, the height of the first bifurcation, canopy diameter, stem diameter, leaf length, and leaf width were evaluated when the plants showed the first mature fruit after completing their development. The quantitative descriptors referring to flowers were corolla length, petal diameter, anther length, and filament length, evaluated when the plants showed 50% flowering. The following fruit descriptors were evaluated when 50% of the fruits were mature: fruit weight, fruit length, largest fruit diameter, smallest fruit diameter, pedicel length, pericarp thickness, placenta length, number of seeds per fruit), and dry matter content.

The experimental design was completely randomized. In the genetic analysis of means and variances, the generation assay was performed with the parents (P_1 and P_2; n=5), the F_1 generation (n=20), the F_2 generation (n=88), and the backcrosses: BC_1 (n=40) and BC_2(n=40).

The data obtained were subjected to generation analysis by estimating the means, phenotypic variances (σ_f^2), environmental variances (σ_m^2), genetic variances (σ_g^2), additive variances (σ_a^2), and the variance due to dominance effects (σ_d^2). The broad-sense heritability (h_a^2) and narrow-sense heritability (h_r^2) estimates were also calculated (Cruz & Regazzi, 1994).

For the complete model, the effects of the mean of all possible homozygotes (m), additive effects (a), dominant effects (d), and epistatic effects were also estimated: additive x additive (aa), additive x dominant (ad), and dominant x dominant (dd). The additive-dominant model included the estimation of additive effects (a), dominant effects (d), and effects of the mean (m). All effects of both models were subjected to the t-test at 1% significance, and when not significant at this level, the 5% significance level was considered. All analyses were performed using the software Genes (Cruz, 2006).

Results and Discussion

Generation means

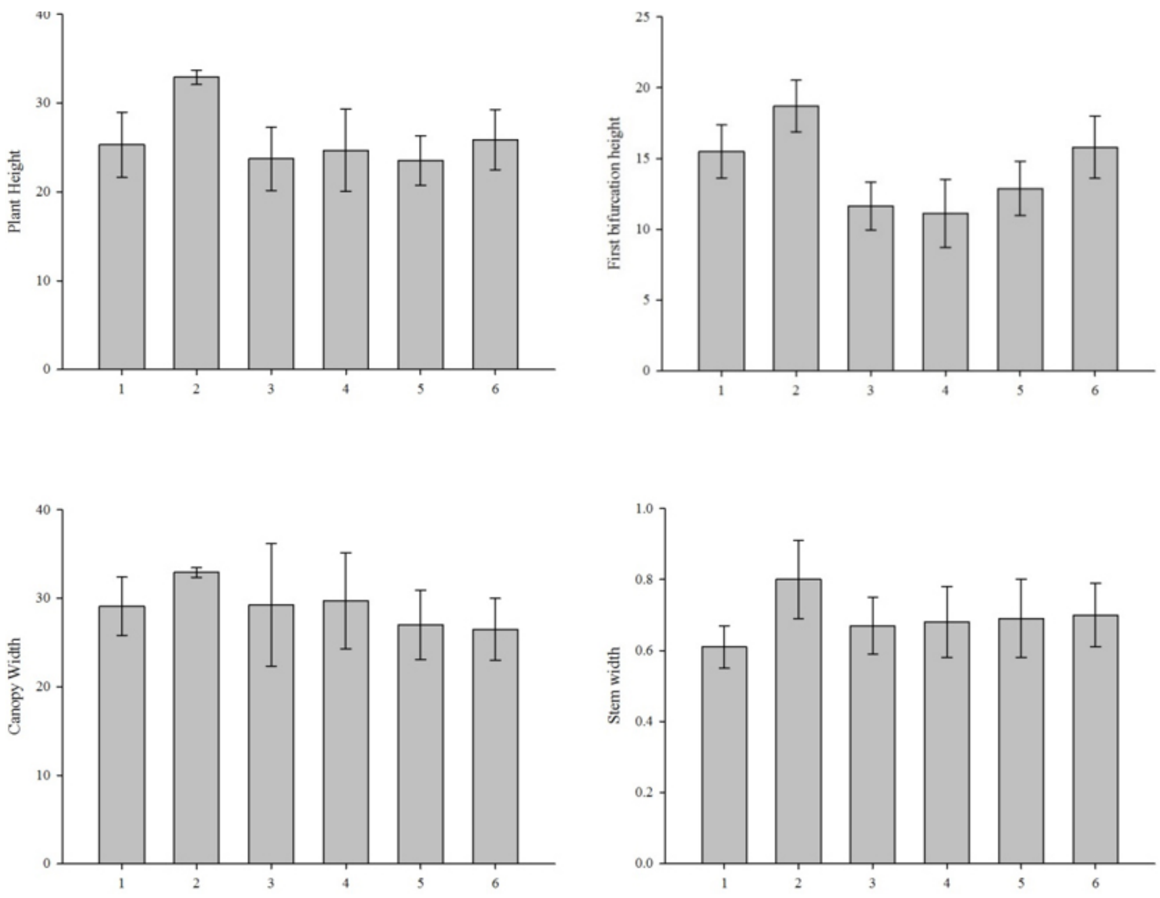
The F_1 generation showed negative heterosis for plant height, height of the first bifurcation, leaf length, leaf width, anther length, smallest fruit diameter, pedicel length, and pericarp thickness (Table 2, Figure 1) since the mean of the F_1 generation was lower than the mean of the parents, indicating an allelic interaction of negative overdominance. For plant height, height of the first bifurcation, leaf length, leaf width, and smallest fruit diameter, this interaction is interesting for ornamental pepper breeding since smaller plants are best fit for pot cultivation, and the use of hybrid for these traits is also recommended. Santos et al. (2014) obtained similar results for plant height in *Capsicum annuum*.

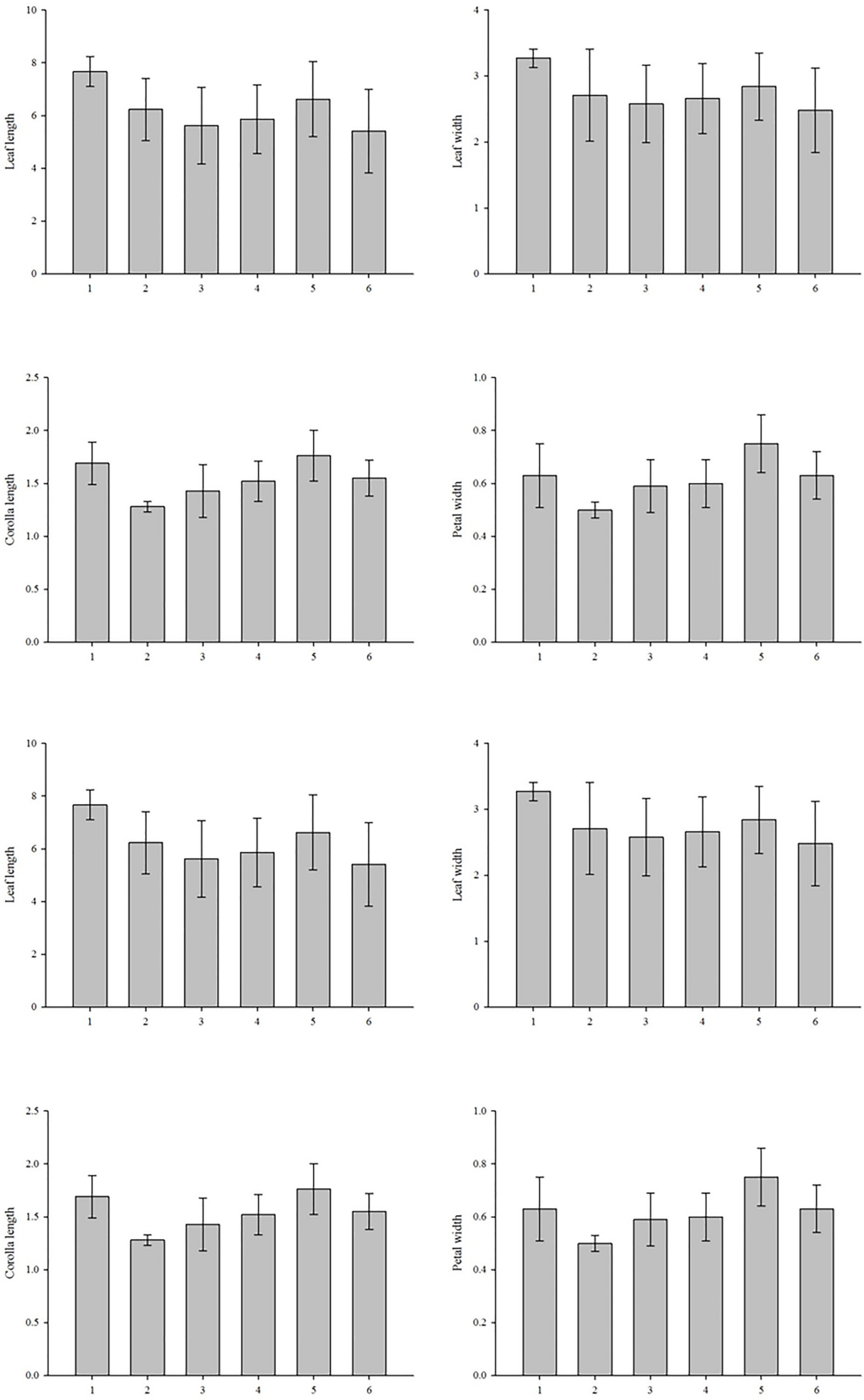
Table 2. Mean values and standard deviation of nineteen quantitative traits referring to plant, flower, and fruit in parents (P_1 and P_2; n=5), F_1 (n=20), F_2 (n=88), and backcrosses (BC_1 and BC_2, n=40) obtained from the *Capsicum annuum* accessions UFPB 349 and UFPB 356.

Generation	PH	HFB	CD	SD	LL	LW	CL	PD	AL	FL
P_1	25.3 ± 3.68	15.5 ± 1.87	29.1 ± 3.29	0.61 ± 0.06	7.67 ± 0.57	3.27 ± 0.14	1.69 ± 0.20	0.63 ± 0.12	0.28 ± 0.02	0.34 ± 0.02
P_2	32.9 ± 0.82	18.7 ± 1.82	32.9 ± 0.55	0.80 ± 0.11	6.23 ± 1.18	2.71 ± 0.70	1.28 ± 0.05	0.50 ± 0.03	0.26 ± 0.06	0.46 ± 0.07
F_1	23.7 ± 3.55	11.65 ± 1.68	29.25 ± 6.90	0.67 ± 0.08	5.62 ± 1.45	2.58 ± 0.59	1.43 ± 0.25	0.59 ± 0.10	0.25 ± 0.04	0.47 ± 0.08
F_2	24.7 ± 4.66	11.12 ± 2.39	29.70 ± 5.41	0.68 ± 0.10	5.87 ± 1.30	2.66 ± 0.53	1.52 ± 0.19	0.60 ± 0.09	0.26 ± 0.03	0.46 ± 0.07
BC_1	23.5 ± 2.77	12.89 ± 1.90	27.01 ± 3.93	0.69 ± 0.11	6.62 ± 1.42	2.84 ± 0.51	1.76 ± 0.24	0.75 ± 0.11	0.29 ± 0.03	0.51 ± 0.06
BC_2	25.9 ± 3.39	15.80 ± 2.19	26.49 ± 3.49	0.70 ± 0.09	5.41 ± 1.59	2.48 ± 0.64	1.55 ± 0.17	0.63 ± 0.09	0.26 ± 0.02	0.48 ± 0.07

Generation	FW	FRL	LFD	SFD	PL	PT	PLL	NSF	DMC
P_1	5.88 ± 1.00	3.39 ± 0.50	1.65 ± 0.16	0.66 ± 0.10	1.27 ± 0.16	0.13 ± 0.01	2.51 ± 0.22	43.4 ± 16.05	10.57 ± 1.78
P_2	0.62 ± 0.13	0.79 ± 0.08	0.61 ± 0.06	0.36 ± 0.07	1.45 ± 0.34	0.08 ± 0.03	0.68 ± 0.17	22.33 ± 2.62	17.25 ± 9.96
F_1	2.67 ± 0.78	1.42 ± 0.53	0.73 ± 0.27	0.34 ± 0.12	1.11 ± 0.38	0.06 ± 0.02	1.05 ± 0.37	49.7 ± 12.56	14.49 ± 3.23
F_2	2.22 ± 0.98	1.57 ± 0.43	0.89 ± 0.20	0.45 ± 0.14	1.37 ± 0.36	0.11 ± 0.06	1.22 ± 0.33	36.05 ± 13.50	15.54 ± 4.70
BC_1	2.68 ± 0.79	2.10 ± 0.33	1.03 ± 0.19	0.44 ± 0.07	1.44 ± 0.24	0.10 ± 0.03	1.65 ± 0.26	47.67 ± 10.72	17.21 ± 3.95
BC_2	1.24 ± 0.59	1.20 ± 0.36	0.75 ± 0.16	0.38 ± 0.08	1.27 ± 0.36	0.08 ± 0.04	0.95 ± 0.28	29.05 ± 8.80	15.26 ± 5.50

PH – Plant height, HFB – Height of the first bifurcation, CD – Canopy diameter, SD – Stem diameter, LL – Leaf length, LW – Leaf width, CL – Corolla length, PD – Petal diameter, AL – Anther length, FL – Filament length, FW – Fruit weight, FRL – Fruit length, LFD – Largest fruit diameter, SMD - Smallest fruit diameter, PL – Pedicel length, PT – Pericarp thickness, PLL – Placenta length, NSF – Number of seeds per fruit, and DMC – Dry matter content.





Leaf length
Leaf width
Corolla length
Petal width
Leaf length
Leaf width
Corolla length
Petal width

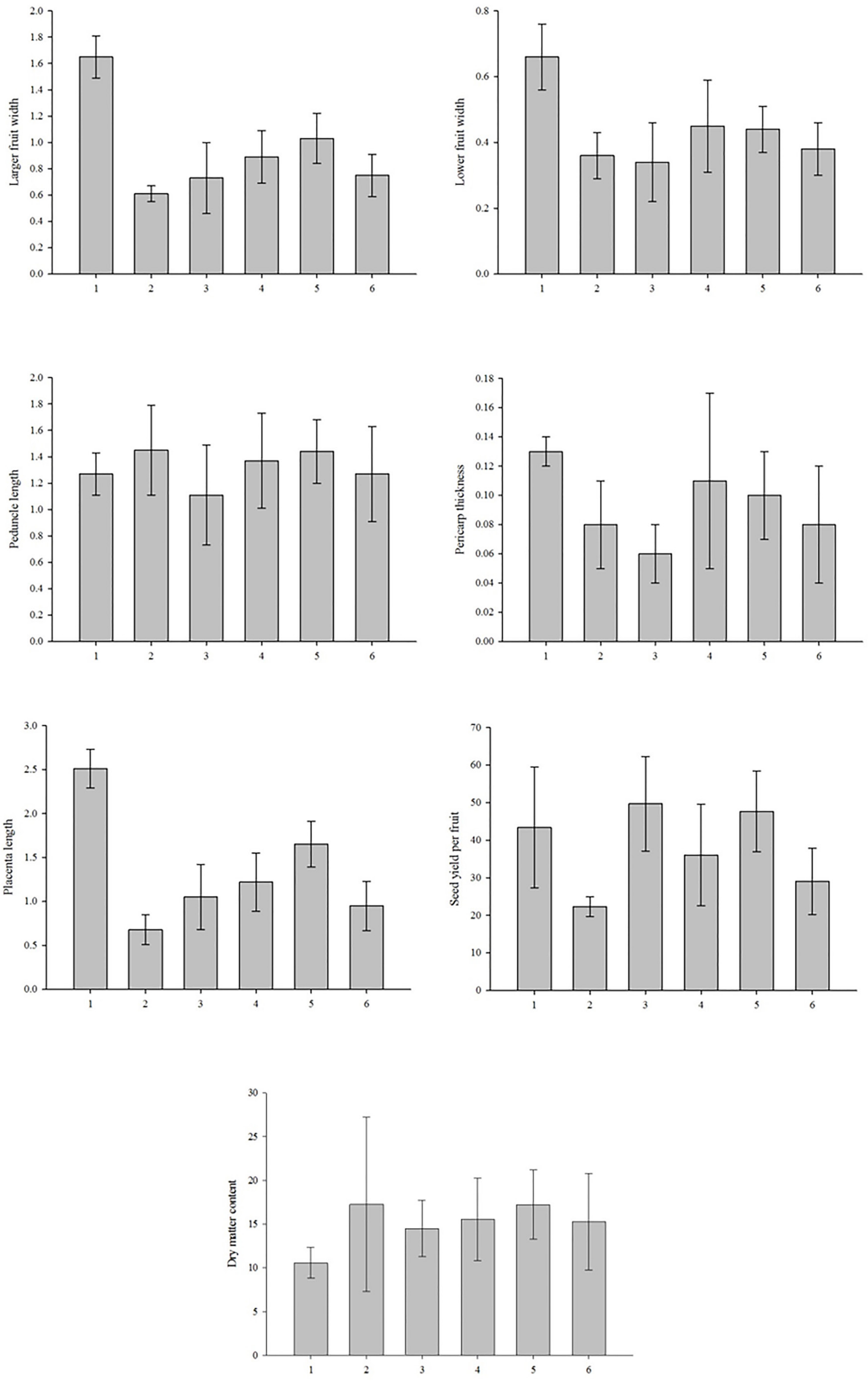


Figura 1. Média e desvio padrão de dezenove caracteres morfoagronômicos em uma população segregante de pimenteira ornamental (*Capsicum annuum* L.), obtida a partir do cruzamento entre os acessos de UFPB 349 e UFPB 356.
1 - P_1; 2 - P_2; 3 - F_1; 4 - F_2; 5 - RC_1; 6 - RC_2.

Positive heterosis was observed for filament length and the number of seeds per fruit, which showed mean values in the F_1 generation higher than the mean of the parents (Table 2). For these traits, the allelic interaction showed overdominance, suggesting that hybrids are the most indicated method to improve them (Barroso et al., 2015). The superiority of F_1 in relation to the parents could be due to the greater accumulation of favorable dominant alleles (Marame et al., 2009).

The mean values of canopy diameter, stem diameter, corolla length, petal diameter, fruit weight, fruit length, largest fruit diameter, placenta length, and dry matter content in the F_1 generation were intermediate in relation to the parents (Table 2, Figure 1), demonstrating an additive allelic interaction for these traits. Therefore, selection in early generations can improve these traits. Santos et al. (2014) observed similar results in *Capsicum annuum* for stem diameter and fruit length in a study describing the presence of an additive allelic interaction for most evaluated traits.

Stem diameter, petal diameter, anther length, and filament length showed mean values in the F_2 generation close to the F_1 means (Table 2, Figure 1), which is expected when there is an additive interaction. For the height of the first bifurcation, fruit weight, and the number of seeds per fruit, the means of the F_2 generation were lower than those of F_1 (Table 2, Figure 1), which is expected when there is an overdominant or dominant interaction. Furthermore, the other traits showed higher mean values in the F_2 generation than most hybrids.

Transgressive individuals in the F_2 generation were observed for plant height, height of the first bifurcation, canopy diameter, leaf length, pedicel length, pericarp thickness, and the number of seeds per fruit. According to Marame et al. (2009), transgression can occur in segregating populations due to the wider genetic distance between genotypes and their parents.

Plant height and the height of the first bifurcation showed transgressive individuals for minimum values in the F_2 generation (Table 2, Figure 1). Therefore, the selection of these individuals is recommended since one of the main objectives of ornamental pepper breeding programs is to obtain smaller plants (Rêgo et al., 2009; Santos et al., 2014). Canopy diameter showed transgressive individuals for maximum and minimum values in the F_2 generation (Table 2, Figure 1), and the selection of individuals with minimum values is recommended since plants with height and canopy diameter proportional to the pot size maintain the harmony between plant architecture and the pot size (Barroso et al. 2012).

Leaf length showed transgressive individuals only for minimum values in the F_2 generation (Table 2, Figure 1), and the selection of these individuals is recommended. Smaller leaves proportional to their canopy are more desirable for ornamental purposes since they allow flowers and fruits to stand out amid the foliage.

Pericarp thickness showed transgressive individuals only for maximum values in the F_2 generation (Table 2, Figure 1), and selection is recommended for this trait since fruits with thicker pericarps are more resistant to the damage caused by post-harvest handling and transport (Lannes et al., 2007; Rêgo et al., 2009).

Transgressive individuals only for minimum values in the F_2 generation were observed for placenta length and the number of seeds per fruit (Table 2, Figure 1), and selection for these traits is not recommended. Fruits with more seeds facilitate the propagation of the species and are more interesting for breeding programs.

For most traits, the backcrosses (BC_1 and BC_2) showed mean values close to those of their respective recurrent parents (Table 2), confirming the choice of parents for these traits (Bnejdi et al., 2009).

Variance components

Stem diameter, corolla length, filament length, fruit weight, fruit length, largest fruit diameter, smallest fruit diameter, placenta length, and the number of seeds per fruit showed higher environmental variance than genetic variance (Table 3), suggesting that these traits were highly influenced by the environment. For these traits, the transmission of the desirable phenotype to the descendants might not be accurate, and the selection of these genotypes based on their phenotype is not reliable (Barroso et al. 2015). The increase in genetic variance could be an alternative to decrease the environmental variance of these traits. Populations formed by the cross between divergent parents showed higher genotypic variance, showing higher heritability values (Borém & Miranda, 2013).

For plant height and pericarp thickness, the genetic variance was superior to environmental variance, suggesting that most of the phenotypic variation observed for these traits have a genetic nature and can be transmitted to the descendants.

Plant height, filament length, fruit weight, fruit length, largest fruit diameter, smallest fruit diameter, pericarp thickness, placenta length, and the number of seeds per fruit showed negative dominance variance, considered zero. According to Moreira et al. (2013), the negative dominance variance values may be related to the low accuracy of the environmental variance estimates. Similar results were observed by Bento et al. (2016) in *Capsicum baccatum* for the number of fruits per plant and pulp thickness and by Bnejdi et al. (2009) for the resistance to *Phytophthora nicotianae* in *Capsicum annuum*. The additive effects were responsible for expressing these traits, allowing new varieties in segregating populations based on the cross between the tested genotypes (Rêgo et al., 2012b). The most suitable method for improving these traits is selection in early generations (Fortunato et al., 2015).

Table 3. Estimation of the genetic parameters based on the variances of morpho-agronomic traits evaluated in a segregating population of ornamental pepper plants (*Capsicum annuum*) obtained from accessions UFPB 347 and UFPB 356.

Genetic parameters	Traits					
	PH	SD	CL	FL	FW	FL
σ^2_f	21.6864	0.0095	0.0371	0.0051	0.9587	0.1829
σ^2_m	8.9471	0.0079	0.0342	0.0039	0.5424	0.1789
σ^2_g	12.7392	0.0016	0.0029	0.0012	0.4164	0.0039
σ^2_a	26.0651	0	0	0.0032	0.9837	0.0179
σ^2_d	0	0.0026	0.0032	0	0	0
h^2_a	58.7430	16.7213	7.7912	23.3229	43.4286	2.1436
h^2_r	58.7430	0	0	23.3229	43.4286	2.1436
GMD	0	0	0	0	0	0

	LFD	SFD	PT	PLL	NSF
σ^2_f	0.0395	0.0199	0.0041	0.1115	182.1419
σ^2_m	0.0351	0.0104	0.0004	0.0713	140.7828
σ^2_g	0.0044	0.0095	0.0037	0.0403	41.3591
σ^2_a	0.0364	0.0311	0.0061	0.1085	180.4861
σ^2_d	0	0	0	0	0
h^2_a	11.1734	47.7420	89.0538	36.1022	22.7071
h^2_r	11.1734	47.7420	89.0538	36.1022	22.7071
GMD	0	0	0	0	0

PH - Plant height, SD - Stem diameter, CL - Corolla length, FL - Filament length, FW - Fruit weight, FRL - Fruit length, LFD - Largest fruit diameter, SFD - Smallest fruit diameter, PT - Pericarp thickness, PLL - Placenta length, and NSF - Number of seeds per fruit. σ^2_f - Phenotypic variance, σ^2_m - Environmental variance, σ^2_g - Genotypic variance, σ^2_a - Additive variance, σ^2_d- Dominance variance, h^2_a – broad-sense heritability, h²r – narrow-sense heritability, GMD- average degree of dominance

The negative additive variance was observed for stem diameter and corolla length and was considered equal to zero. For these traits, dominance genetic effects were responsible for expressing the trait, and the production of hybrids is recommended since the heterozygotes will have the same value as the dominant homozygote. The predominance of dominant genetic effects complicates the works of plant breeders (Bnejdi et al., 2009) since it is not possible to guarantee that the superior phenotype observed corresponds to the desired genotype (Bento et al., 2013). Bento et al. (2016) reported the presence of negative additive variance for the content of total soluble solids in *Capsicum annuum*. These traits can be improved through selection in advanced generations using the SSD method (single seed descent), which allows a rapid generation advance for later genotype selection (Bento et al., 2013).

Plant height and pericarp thickness showed high broad-sense heritability, with 58.74% and 89.05%, respectively (Table 3). Heritability is the proportion of total phenotypic variance in a population attributed to genetic effects (Yang et al., 2017). The higher the heritability, the higher the genetic variance, and, consequently, the lower the environmental influence, allowing genetic gains through selection in early generations (Pessoa et al., 2015; Silva Neto et al., 2014). Costa et al. (2016) described the existence of high broad-sense heritability for fruit weight, fruit length, and pericarp thickness. In another study, Fortunato et al. (2015) observed high broad-sense heritability for corolla length and petal diameter, and Nascimento et al. (2012) reported high broad-sense heritability for corolla length, suggesting that genetic variation was responsible for most of the total variability of this trait and can be transmitted to the descendants.

Broad-sense heritability showed intermediate values for the traits of fruit weight and smallest fruit diameter (Table 3), suggesting that their variations were due to genetic and environmental causes. On the other hand, broad-sense heritability was low for stem diameter, corolla length, filament length, fruit length, largest fruit diameter, placenta length, and the number of seeds per fruit (Table 3), suggesting that these traits are more influenced by environmental components and complicating their selection (Passos et al., 2010; Silva Neto et al., 2014). An alternative to improve these traits is performing selection in advanced generations (Rêgo et al., 2009a) or indirect selection based on a strongly correlated secondary trait with high heritability (Rêgo et al., 2011).

The traits of plant height, filament length, fruit weight, fruit length, largest fruit diameter, smallest fruit diameter, pericarp thickness, placenta length, and the number of seeds per fruit showed narrow-sense heritability equal to broad-sense heritability. The dominance variance was negative in these traits, indicating that all the genetic variance observed was due to the additive genetic variation (Bento et al., 2016).

High narrow-sense heritability values were observed for plant height and pericarp thickness (Table 3), suggesting the predominance of additive genetic effects in their expression. Narrow-sense heritability refers to the proportion of phenotypic variance attributable only to additive genetic variation, excluding the contribution due to dominance effects and epistasis (Yang et al. 2017). Satisfactory gains for these traits can be obtained in segregating generations (Medeiros et al., 2014) by performing selection in early generations (Fortunato et al., 2015).

Fruit weight and the smallest fruit diameter showed intermediate narrow-sense heritability values (Table 3), highlighting the importance of additive genetic effects and genetic effects of dominance and/or epistasis. For these traits, reciprocal recurrent selection or selection between and within half-sib families is recommended, exploring both the additive and non-additive genetic variances.

The traits of filament length, fruit length, largest fruit diameter, placenta length, and the number of seeds per fruit showed low narrow-sense heritability (Table 3), highlighting the low reliability of the genotypes in transmitting the desired phenotype to their progeny (Gonçalves et al., 2011). For these traits, selection in early generations is not recommended, favoring selection in advanced generations (Bento et al., 2013) or the use of hybrids (Barroso et al., 2015).

The narrow-sense heritability for corolla length was equal to zero (Table 3). This trait showed a negative additive variance, which was considered zero, suggesting the predominance of dominance and/or epistatic genetic effects controlling the trait.

Generation analysis

The additive-dominant model (m, a, d) satisfactorily explained the genetic parameters of most traits since these showed coefficients of determination (R^2) above 70% (Table 4).

Table 4. Genetic effects for the complete and additive-dominant models in plant, flower, and fruit traits of ornamental pepper plants (*Capsicum annuum*).

Effects	PH		SD		CL		FL		FW		FRL	
	Estimate	R^2 (%)	Estimate	R^2 (%)	Estimate	R^2 (%)	Estimate	R^2 (%)	Estimate	R^2 (%)	Estimate	R^2 (%)
Complete Model												
m	29.01**	81.92	0.62**	80.71	0.95**	36.19	0.25**	25.80	4.30**	21.60	1.78**	23.95
a	-3.8**	12.95	-0.09*	10.13	0.20**	14.16	-0.06**	11.90	2.63**	50.79	1.30**	70.33
d	-11.99ns	2.30	0.17ns	0.88	1.80**	17.69	0.60**	20.60	-6.67**	8.16	-0.50ns	0.27
aa	0.09ns	0.001	0.08ns	1.70	0.53**	12.52	0.15**	9.85	-1.05*	1.53	0.31ns	0.86
ad	2.91ns	1.14	0.17*	5.53	0.01ns	0.004	0.18**	14.89	-2.38**	7.09	-0.80**	4.53
dd	6.70ns	1.69	-0.12ns	1.03	-1.32**	19.44	-0.37**	16.96	5.04**	10.82	0.14ns	0.04
Additive-dominant model												
m	28.71**	96.65	0.69**	99.53	1.52**	97.63	0.39**	95.41	2.23**	63.51	1.83**	73.11
a	-3.81**	1.91	-0.04*	0.46	0.22**	2.30	-0.03*	0.62	1.63**	36.47	1.03**	25.93
d	-6.87**	1.44	-0.01ns	0.007	0.08ns	0.07	0.15**	3.97	-0.08ns	0.02	-0.42**	0.96
r	0.9582		0.9012		0.8277		0.7104		0.9306		0.9851	

Effects	LFD		SFD		PT		PLL		NSF	
	Estimate	R^2 (%)	Estimate	R^2 (%)	Estimate	R^2 (%)	Estimate	R^2 (%)	Estimate	R^2 (%)
Complete Model										
m	1.15**	29.90	0.67**	61.13	0.18**	51.34	1.29**	16.33	23.63**	36.27
a	0.52**	62.04	0.15**	20.52	0.03**	25.03	0.91**	80.22	10.53*	35.73
d	-0.61ns	1.21	-0.55**	7.04	-0.18*	9.75	-0.04ns	0.002	23.61ns	5.49
aa	-0.02ns	0.01	-0.16*	4.19	-0.08*	10.14	0.31ns	1.05	9.24ns	6.94
ad	-0.49**	6.61	-0.16*	4.63	-0.01ns	0.20	-0.42*	2.27	16.16ns	15.43
dd	0.19 ns	0.22	0.22ns	2.49	0.07ns	3.54	-0.19ns	0.12	2.46ns	0.13
Additive-dominant model										
m	1.05**	82.71	0.49**	92.11	0.11**	91.55	1.54**	70.47	34.59**	83.80
a	0.40**	15.54	0.08**	5.58	0.02**	3.47	0.80**	27.21	13.63**	14.89
d	-0.30**	1.75	-0.15**	2.30	-0.04**	4.97	-0.54**	2.32	7.95*	1.30
r	0.9798		0.9623		0.9122		0.9937		0.9158	

PH - Plant height, SD - Stem diameter, CL - Corolla length, FL - Filament length, FW - Fruit weight, FRL - Fruit length, LFD - Largest fruit diameter, SFD - Smallest fruit diameter, PT - Pericarp thickness, PLL - Placenta length, and NSF - Number of seeds per fruit. m - mean of homozygotes, a - additive, d - dominant, aa - additive x additive, ad - additive x dominant, and ad- additive x dominant, r – correlation coefficient. *, ** significant values other than zero by the t-test at 5% and 1% probability, ns – non-significant.

In the additive-dominant model, the mean of all possible homozygotes (m) was significant at 1% probability for all evaluated traits (Table 4). The additive genetic effects (a) were significant for all traits at 1% and 5% probability by the t-test. Most traits showed significant dominance effects (d) at 1% probability. For the number of seeds per fruit, dominance effects (d) were significant at 5% probability. Stem diameter, corolla length, and fruit weight showed non-significant dominance effects (d) (Table 4).

The additive genetic effects were more important than dominance effects for fruit length, largest fruit diameter, placenta length, and the number of seeds per fruit. For stem diameter, corolla length, and fruit weight, only the additive genetic effects are involved in trait expression. For these traits, selection can be performed in the first generations for a higher likelihood of genetic gain (Medeiros et al., 2014). Breeding methods based on selection or backcrossing can be more effective when additive genetic effects are predominant (Rêgo et al., 2009a; 2015; Rêgo & Rêgo, 2016).

The other traits showed a predominance of dominant genetic effects in their control, for which the recommended methods are selection in advanced generations, use of hybrids (Fortunato et al., 2015; Rêgo et al., 2009a; 2015; Rêgo & Rêgo, 2016), or selection in advanced generations using more complex methods, e.g., Pedigree or recurrent selection (Rêgo et al., 2009a; 2015; Rêgo & Rêgo, 2016).

Conclusions

Plant height and pericarp thickness showed high narrow-sense heritability, with 58.74 and 89.05, respectively, suggesting the predominance of additive genetic effects in their expression.

The additive-dominant model showed adjustments over 70%, explaining the genetic parameters of almost all evaluated traits and suggesting that only the additive and dominant genetic effects influenced the control of these traits.

Stem diameter, corolla length, and fruit weight showed only additive genetic effects. For fruit length, largest fruit diameter, placenta length, and the number of seeds per fruit, the additive genetic effects were more important than dominance effects, and selection in early generations is recommended to improve these traits.

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